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ORIGINAL ARTICLE

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Keywords Human-provided foods · Florida scrub-jay · Nestling diet · Diet switching · Urbanization

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Introduction

Birds adjust timing of breeding so that peak availability of food coincides with nestling rearing, and birds that do so have the highest reproductive success (e.g., Thomas et al. 2001). Therefore, food choices for provisioning the young are important for reproductive success. Many birds switch from an omnivorous diet to an arthropod diet because nestlings depend on high-quality arthropod foods to maximize growth (Krebs 1978). This switch is predicted by optimal diet choice models, which state that if a high-quality food type is common, lower quality foods will be ignored (Stephens and Krebs 1986). Parents should include lower quality foods in the nestling diet only when brood demand is higher than expected as a consequence of unpredictable environments, periods of depressed foraging conditions, or other unpredictable reductions in parental foraging ability (Wright et al. 1998). Many studies describe the relationship between diet composition and food availability (e.g., Rauter et al. 2000; Annett and Pierotti 1989). These studies often show an increase in food selectivity when food is readily available; however, few experimental studies have tested the conditions under which low-quality food is fed to nestlings (e.g., Wright et al. 1998).

Comparative studies between urban and wildland habitats provide a unique opportunity to study food preference in relation to food availability, because food availability during nestling rearing can differ strongly between these habitats. In wildland habitats, arthropods are abundant during nestling rearing. In urban habitats, human-

provided foods, such as birdseeds, nectar from exotic vegetation, garbage, or pet food are the most abundant and spatially and temporally predictable food, while arthropod abundance tends to decline (McIntyre 2000). In addition, competition for arthropod foods might generally be higher in urbanized areas than in wildlands, because bird densities are higher in these areas (Shochat et al. 2004) and because the high food abundance during winter attracts birds who often remain and breed (Solonen 2001). Some studies suggest that human-provided foods reduce reproductive success (Annett and Pierrotti 1999; Belant et al. 1998; Boal and Mannan 1999). Most human-provided foods are plant-based and, as such, are harder to digest (Karasov 1990; Buchsbaum et al. 1986; Jakubas et al. 1995) and often have lower water content (e.g., birdseeds, Diaz 1989) than animal foods. Given that nestlings have poorer digestive capabilities (Caviedes-Vidal and Karasov 2001) and greater water requirements than adults (Robbins 1983), plant-based foods may not be of sufficient quality to maintain the fast growth rates characteristic of nestling passerines. In support, zebra finch nestlings (*Taeniopygia*, *guttata*) grew more slowly on a plant-based diet than did control nestlings fed a natural mixed diet (Birkhead et al. 1999). Optimal foraging models predict changes in diet choices in response to changes in food encounter rates. In urban habitats, the rate at which a foraging bird encounters arthropods likely decreases, while the rate at which it encounters human-provided foods increases. As a consequence, we might expect urban parents to feed human-provided foods to nestlings because of the increased costs of finding scarce arthropods, even though this might decrease nestling growth.

In wildland habitat, Florida scrub-jays (*Aphelocoma*, *coeurulescens*) feed their young exclusively arthropods, especially orthopterans and lepidopteran larvae (Stallcup and Woolfenden 1978). In suburban habitat, the abundance of arthropods per oak stem is less than half that in the wildland habitat and fewer oak stems exist because of loss of the native scrub habitats (Shawkey et al. 2004). In addition, approximately 15% of the nestling diet is human-provided (Sauter et al., in preparation). Suburban nestlings have reduced growth and survival compared to wildland nestlings, which might result from limited availability of arthropod food or inclusion of plant-based human-provided foods (Shawkey et al. 2004).

What explanations does optimal foraging theory offer for the inclusion of human-provided foods into nestling diet despite the apparent costs? First, the optimal foraging theory assumes that the forager can assess the quality and availability of the foods; however, we do not know whether this is true with respect to the distinction between natural and human-provided foods in suburban Florida scrub-jays. Scrub-jays are omnivorous (Woolfenden and Fitzpatrick 1996). Wildland jays consume acorns throughout the winter and spring (DeGange 1976) but feed their nestlings exclusively arthropods. This suggests that they can

Table 1 Hypotheses and predictions tested

Hypotheses tested		Predictions	
Experiment 1			
1) Discrimination	Jays' food choice is influenced by changing nutritional needs.	1.a	Pre-breeding parents will show little preference for animal versus plant foods.
		1.b	At the onset of breeding, preference for natural foods will increase.
		1.c	The increased preference for natural foods will occur earlier in females than in males
		1.d	During nestling rearing, preference for natural foods will be greatest.
Experiment 2			
2) Food availability	Jays' food choice is influenced by the availability of natural foods.	2.a	Suburban parents should show a stronger preference for natural foods than wildland parents.
		2.b	Food supplementation should decrease the preference for natural foods.
		2.c	When feeding nestlings, preference for natural foods will always be greater than when self-feeding regardless of food availability.
3) Time constraints	Jays' food choice is influenced by time constraints.	3.a	Preference for natural foods decreases with increasing handling time in both habitats.
		3.b	When feeding nestlings, food choices are less affected by time constraints than when self-feeding.

discriminate between plant and animal foods; however, we do not know if this is true for novel food types (from an evolutionary perspective), such as the human-provided foods in suburban habitats. Second, optimal foraging theory predicts that searching and handling time of the foods available influences food choice. If jays can discriminate between food types, their food choice may vary with the availability of the preferred food in the environment, with time and energy constraints of obtaining this food, or both. However, which food type is the preferred one will depend on an individual's nutritional demands. Therefore, food choice also might differ between self-feeding and provisioning young. We designed a series of food choice experiments in which jays chose between natural and human-provided foods. In addition, we manipulated the availability of natural food in the environment by experimental food supplementation, and we manipulated time constraints by increasing the handling time to obtain natural food to test the following hypotheses: 1) Jays do not discriminate between natural and human-provided foods; 2) If jays do discriminate between natural and human-provided foods, then food choice is influenced by the availability of natural foods; or 3) If jays do discriminate between natural and human-provided foods, then food choice is influenced by time constraints on obtaining preferred foods.

These hypotheses are not mutually exclusive but generate a series of testable predictions (Table 1). To test the assumption of the optimal foraging theory that jays can discriminate among foods (hypothesis 1), we conducted food trials during three different annual periods when the nutritional demands of the adults differ (experiment 1). We expected that if jays do discriminate they would alter their food choice relative to their nutritional demands (predictions 1.a, 1.b, and 1.d). During oogenesis, females require additional protein, fat, and selected micronutrients (Carey 1996; Ramsay and Houston 1997), which are acquired more easily through animal- than plant-based foods (Karasov 1990); thus, we also predict that if jays can discriminate, females should switch from human-provided food to natural food when producing eggs, whereas, males will not switch until their nutritional demands change, when they start feeding young. We expect the shift in food preference from human-provided foods to natural foods to occur earlier in females than in males (prediction 1.c).

If jays discriminate among foods, environmental constraints in the nestling stage might cause parents to switch back to lower-quality human-provided food despite their preference for natural foods and the apparent costs of this food choice. We tested whether variation in food availability (hypothesis 2), time constraints (hypothesis 3), or both, cause parents to change food choices in a second experiment. Hypothesis 2 predicts that because natural foods are preferred in both habitats, but in more limited availability in the suburbs, that when given a simultaneous choice between human-provided and natural food (prediction 2.a, Table 1), suburban birds should show a stronger preference because they have less of an option of obtaining natural foods from their environment. Similarly, parents that are experimentally supplemented with food, should perceive greater availability of food in the environment than those not provided supplemental food and, thus, show less of a preference for natural foods and be willing to work less to obtain natural food at the feeder when given a simultaneous choice between human-provided and natural food (prediction 2.b, Table 1). Hypothesis 3 predicts that time constraints also are important in determining parental food choices. Consequently, we expect that by experimentally increasing the handling time for the preferred food we might at the same time decrease the preference for this food (prediction 3.a). In addition, because the costs of diet switching are greater when feeding nestlings than when self-feeding (Wright et al. 1998), we expect the food choices of adults in our experimental treatment to differ depending on whether they were self-feeding or feeding nestlings (predictions 2.c and 3.b, Table 1).

Materials and methods

Study organism Florida scrub-jay groups consist of a socially and genetically monogamous breeding pair and from zero to six non-breeding helpers. The birds breed cooperatively and defend year-round all-purpose territories. Males do not incubate the eggs or brood nestlings, but provide food to both the breeding female and young. Females brood young, but increase their provisioning rate throughout the later half of the nestling period. Helpers provide some food to nestlings and fledglings, and assist in nest defense (for references and further information on the species see Woolfenden and Fitzpatrick 1996). The Florida scrub-jay is the only bird species endemic to Florida and is federally listed as Threatened. At present, more than 30% of Florida scrub-jay populations occur in urban habitats (Breininger 1999).

Study population We studied food preference of Florida scrub-jays in suburban and wildland habitats of Highlands County, Florida. The suburban study site was located at Placid Lakes Estates (27°10′ N, 81°24′ W), a residential housing subdivision near Lake Placid (for details, see Bowman and Woolfenden 2001, 2002). In this site, the native scrub vegetation occurs as patches within a matrix of roads and human housing. Human-provided foods are available in the suburbs year-round. The wildland study site is at Archbold Biological Station (for details, see Mumme 1992; Schoech et al. 1996), approximately 10–12 km south of the suburban site. In this natural preserve, the scrub vegetation is part of a heterogeneous landscape of periodically burned habitats, including xeric oak scrub, scrubby flatwoods, rosemary balds, and seasonal ponds (Abrahamson et al. 1984). Wildland scrub-jays occasionally receive peanut bits by researchers and visitors, but the amount they receive is considered inconsequential to their energy budget (Fleischer et al. 2003). All birds of both populations are individually color banded and the sex, social status (breeder, nonbreeder), and nest status

(building, incubating, brooding) of each jay are known from ongoing long-term studies on the demography of the two populations (Schoech et al. 1996; Bowman and Woolfenden 2001). Although sexually monomorphic, all birds are sexed based on behavior (hiccup call, female-only incubation, Woolfenden and Fitzpatrick 1996) and, since 1998, by genetic analysis.

Experiment 1: food discrimination (hypothesis 1)

In the first experiment, we tested whether parents were able to discriminate among foods by testing their simultaneous preference between human-provided and natural foods during the pre-breeding and breeding period when nutritional demands of the parents differ. This experiment was conducted between February 12, 2002 and June 13, 2002 in the suburban population only. To avoid measuring the response to a novel food type, we did not test the wildland population because they are not regularly exposed to all the food types offered. The groups tested consisted of breeding pairs without helpers. We tested the birds in each territory up to three times: 1) pre-breeding—1 to 2 weeks before the laying of the first egg (18 trials), 2) mid-incubation—day 9 of incubation (17 trials), 3) brooding—day 12 or 13 post-hatching (seven trials). Trials were performed 2 to 4 h after sunrise. One to 3 days before each trial, a feeder was placed near the activity center of the territory during the pre-breeding phase and 10 to 20 m from the nest during the breeding phase. Jays were familiarized with the experimental setup to avoid measuring the response to a novel situation. The feeder consisted of a 1-m wooden pole, topped with a plastic saucer (diameter 20 cm, Martha Stewart, New York). The foods offered were 60 waxworms (*Galleria mellonella*, Grubco, Hamilton, Ohio, USA; approximately 36 kcal), 20 pieces of white wheat bread (approximately 2 kcal), 20 sunflower seeds (approximately 9 kcal), and 20 peanut pieces (approximately 25 kcal). The nutritional composition and caloric value of these foods are shown in Table 2. The human-provided foods (peanuts, bread, and sunflower seeds) were chosen to reflect foods available to the suburban jays and to match the total amount and caloric value of the waxworms, which were used as a surrogate for natural foods commonly fed to nestlings (lepidopteran larvae). Each trial started when the first bird landed on the table and ended when the birds had removed 20 items or after 45 min had elapsed. After 20 items, one food type could have been depleted and, therefore, the birds would no longer have a choice among all four food types. Trials with fewer than five items taken were discarded. For each item taken, we recorded the individual jay (from its color bands) and the food item it chose.

Following Alldredge and Ratti (1986), we used a Friedman test on the proportion of each food type taken per breeding stage to determine whether the food types were taken according to their availability. In addition, to determine which resources were preferred or avoided in each of the breeding stages, we calculated Bonferroni's simultaneous confidence intervals (Byers and Steinhorst 1984). Because in many of the trials sunflower seeds and bread were completely avoided, data were skewed preventing the use of analyses of variance. To determine if the number of waxworms taken by each group changed with the breeding stage, we used a Friedman test for related samples. Differences between the sexes were analyzed using a Mann–Whitney *U* test for each breeding stage. Because females came to the feeder less often and took fewer items than males, we compared the proportion of natural items taken by males and females rather than the absolute number of items taken by each sex.

Experiment 2: food choice depending on food availability and/or time constraints (hypotheses 2 and 3)

In the second experiment, we tested whether food availability (hypothesis 2), time constraints (hypothesis 3), or both, cause parents to change food choices. We manipulated food availability in the environment by supplementing groups in both habitats with waxworms during the brooding period. Non-supplemented groups received no waxworms during this period. We performed this experiment between March 29 and May 26, 2003 using a design similar to the first experiment, except that trials were conducted in both the suburbs and wildlands. We tested groups regardless of group size. At hatching, groups in each study area were alternately assigned to the non-supplemented or supplemented treatment. Each day, between day 1 and 10 post-hatching, supplemented groups received 30 g of waxworms. Non-supplemented groups received one peanut broken into pieces as a control for the disturbance of a researcher's visit near the nest. On day 11, we counted the number of nestlings per brood as an indicator of food demand. Next, we conducted food trials

Table 2 Nutritional composition of food types in the food preference experiment

Item	Moisture (%)	Fat (%)	Protein (%)	Kcal/g	Kcal/item	Source
Waxworm	61.73	22.19	15.50	2.77	0.60	Grubco 2004[a]
Peanut	6.50	49.23	25.80	5.67	1.25	About 2004[b]
White bread	36.70	3.60	8.20	0.17	0.45	About 2004[b]
Sunflower seeds (seed kernel)	1.20	49.80	19.32	5.82	0.10	About 2004[b]

[a] http://www.grubco.com

[b] http://www.nutrition.about.com/library/foodfind

similar to those conducted in the first experiment, but we experimentally manipulated the handling time of natural foods during one of the food trials (see below). Between days 12 and 17, we presented each group with a choice between 60 waxworms (13 g, 36 kcal) and 60 pieces of peanuts (6.4 g, 36 kcal). Choice trials were conducted twice for each group; during one of these trials, randomly allocated to first or second trial, we increased the handling time necessary to gather the waxworms from the feeder. One of the two trials tested the food availability hypothesis stating that if the availability of natural foods influences food choice, we expect that food supplemented birds show a lower preference for natural foods than non-supplemented controls. The other of the two trials tested for time constraints: if time constraints influence food choice, we expect that birds switch to low-quality peanuts when the handling time of the natural foods is increased. To increase handling time, we placed waxworms on a 3×50 cm corrugated cardboard strip, which we then rolled tightly. The waxworms were not deeper than 1 cm from the edge of the roll and could easily be extracted from the roll within 1 to 2 s by the jays. The roll was attached to the feeder using cable ties. Before the trials, jays in all groups were trained to extract the waxworms from the rolled cardboard.

Trials were performed 1 to 3 h after sunrise. Each trial started when the first bird landed on the table and ended when all items had been taken or after 45 min had elapsed. For each item taken, we recorded the identity and its fate. Fate of food items was categorized as eaten at the feeder, carried away from the feeder to be eaten elsewhere or cached, or taken to the nest. For analyses of preference at the feeder, we used only the first 60 items taken, because at this time all of a preferred item could have been depleted. For the analyses of the items taken to the nest, we used all items recorded because only 10% of all items chosen at the feeder were taken to the nest, and an item taken at the feeder could always be brought to the nest or not.

We conducted separate analyses for food choices when self-feeding and food choices when feeding nestlings. For food choices when self-feeding, we tested whether the proportion of waxworms chosen at the feeding table was influenced by habitat, supplementation, handling time, or a combination of the preceding using a repeated-measures ANCOVA controlling for brood size and group size. Group identity was the subject, habitat and supplementation were the independent factors, brood size and group size were covariates, handling time (not manipulated/increased) was the within-subjects variable, and the logit-transformed proportion of waxworms taken was the dependent variable. We tested for the interaction between habitat and supplementation.

For food choices when feeding young, we first compared the proportion of waxworms taken at the feeder with the proportion of waxworms fed to young, using a Wilcoxon signed-rank test. To test if the proportion of waxworms taken to the nest varied with habitat, food supplementation, or handling time, we used a combination of non-parametric methods (Mann–Whitney *U* test, Wilcoxon signed-rank tests). The analysis of the proportion of waxworms taken to the nest was done separately for waxworms with and without the increased handling time because data collected from the same group were not independent. ANCOVA could not be applied because various assumptions were violated.

For all analyses in experiment 2, we used two measures of food preference: 1) the proportion of waxworms, i.e., the number of waxworms divided by the number of all items taken per trial, and 2) the strength of the response to the handling time treatment following protocols established by Whelan and Willson (1994). Preference was measured in the following manner. First, birds chose between two food items. Then, we increased the handling time necessary to obtain the preferred food item and measured whether the preference was reversed. The strength of the food preference was measured as the interaction between food type and change in availability (handling time). We used the strength of the response (i.e., the difference in preference for natural foods between the not-manipulated and increased handling time treatment per group) as a preference measure. The strength of preference is the within-subject effect in the repeated measures ANCOVA. No difference meant no diet switch and, therefore, a high preference. All statistical analyses were done using SPSS 11.5 for Windows (SPSS Inc, 2002).

Results

Food discrimination (hypothesis 1)

Florida scrub-jays discriminated among food types in all breeding stages (Fig. 1). During pre-breeding, the use of the food types differed from their respective availability (Friedman test, T=20.66, df=17, P<0.01). Waxworms were avoided, peanuts were preferred, and bread and sunflower seeds were taken according to their availability. During incubation, jays also discriminated among food types (Friedman test, T=7.42, df=16, P<0.01). Waxworms, peanuts, and bread were taken according to their availability, but sunflower seeds were avoided. During nestling rearing, only seven groups were tested because of a high rate of nest failures. Although the proportion of waxworms taken was higher than expected (0.74, expected: 0.50), and the proportion of bread (0.08, expected: 0.17) and sunflower seeds (0.00, expected: 0.17) taken were lower than expected, the differences were not significant, likely as a result of the relatively low sample sizes. Overall, as breeding advanced, birds took an increasing number of waxworms (Friedman test for related samples, N=7, χ^2=5.85, df=2, P=0.05) and a decreasing number of sunflower seeds (N=7, χ^2=6.00, df=2, P=0.05). The number of peanuts (N=7, χ^2=1.87, df=2, P=0.42) and bread items taken (N=7, χ^2=4.44, df=2, P=0.11) did not vary significantly with breeding stage. A difference existed between males and females in their preference for waxworms. During incubation, females showed an earlier preference for natural foods than males: females took a higher proportion of waxworms than males (means±SD,

0.89±0.15 vs 0.47±0.48, respectively; one-tailed Mann–Whitney *U* test, *N*=23, *Z*=−1.86, *P*=0.03) as predicted, but during nestling rearing the proportions did not differ (0.85±0.15 vs 0.71±0.42, respectively; one-tailed Mann–Whitney *U* test, *N*=12, *Z*=0.00, *P*=0.52).

Food choice depending on food availability or time constraints (hypotheses 2 and 3)

We tested whether food choice was influenced by the availability or handling time of the natural food type in a total of 43 groups, 38 of them in both handling time treatments (not manipulated/increased handling time for waxworms, Table 3). In Table 3, between-subjects effects refer to the difference in preference for waxworms depending on habitat and supplementation, whereas, within-subject effects indicate whether the increased handling time for natural foods changes preference for natural foods. Both food supplementation with natural foods and habitat (wildland or suburban) influenced preference for natural foods. Birds provided with supplemental food and suburban birds took a higher proportion of waxworms than non-supplemented (supplementation effect, Table 3) or wildland (habitat effect, Table 3) jays. The proportion of waxworms taken did not depend on the interaction between habitat and supplementation, brood size, or group size.

Handling time also influenced preference for natural foods; jays took more peanuts when handling time for waxworms was increased (Fig. 2, Table 3), even though this experiment was conducted during nestling rearing when waxworms were the main food item taken during our first experiment (Fig. 1). This was true for supplemented and non-supplemented groups in both habitats (Fig. 2, Table 3); however, the decrease in preference for waxworms with increased handling time was smaller in the suburbs than in the wildlands (handling time–habitat effect, Table 3). The change of preference with increased handling time did not depend on the interaction between habitat and supplementation, brood size, or group size.

Ten of 43 groups tested took items to the nest in both handling time treatments. Preference for natural foods that were taken to young differed from overall preferences at the feeder, which included food used for self-feeding. We analyzed the two handling time treatments separately because of statistical considerations (see Materials and methods); however, the results were identical for both treatments. The proportion of waxworms taken to the nest was higher than that of waxworms taken from the feeder (Wilcoxon signed-rank test, not manipulated handling time: *N*=27, *Z*=−3.668, *P*<0.01, increased handling time: *N*=27, *Z*=−3.668, *P*<0.01), i.e., a waxworm taken from the feeder was more likely to be fed to the nestlings than a peanut taken from the feeder. The proportion of waxworms taken to the nest did not differ between sites (Mann–Whitney *U* test, not manipulated handling time: *N*=27, *Z*=−1.118, *P*=0.35, increased handling time: *N*=25, *Z*=−0.176, *P*=0.89) nor between non-supplemented and supplemented groups (Mann–Whitney *U* test, not manipulated handling time: *N*=27, *Z*=−0.176, *P*=0.89, increased handling time: *N*=25, *Z*=−0.205, *P*=0.85). In contrast to the effect of the handling time at the feeder, the preference for waxworms used to feed nestlings was not influenced by increased handling times for obtaining the natural food (Fig. 2b; Wilcoxon signed-rank test, *N*=10, *Z*=−0.420, *P*=0.67). In general, the items taken to the nest consisted of more than 80% waxworms in both habitats and all treatments.

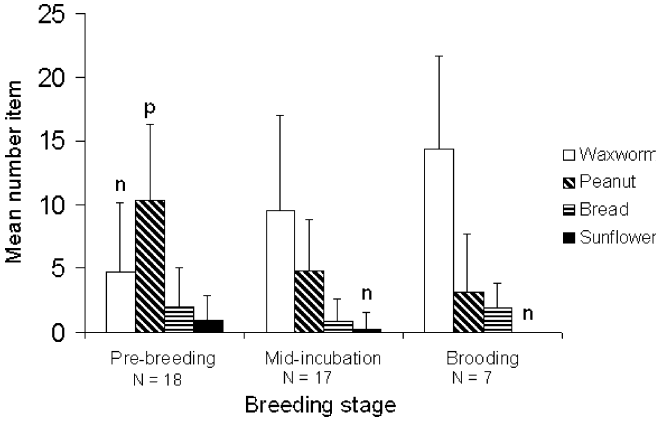

Fig. 1 Mean number (±SD) of each food type taken per breeding stage. '*p*' indicates positive selection, '*n*' indicates negative selection, no sign indicates no selection determined by Bonferroni's simultaneous confidence intervals. *N*=number of groups tested

Discussion

Food discrimination

Parents showed the expected switch in food preference from human-provided foods to arthropods at the onset of breeding. Parents were able to discriminate between human-provided and natural foods and adjust their preferences according to the differing nutritional demands of breeding. In the first experiment, jays avoided sunflower seeds and bread and, with the onset of breeding, exhibited decreased preference for peanuts and an increased preference for waxworms. In the second experiment, jays showed a strong preference for feeding waxworms to nestlings. We can, thus, refute the hypothesis that scrub-jays feed human-provided foods to nestlings because they cannot discriminate between those foods and natural foods. All the human-provided foods are of plant origin, and jays do not normally feed plant foods to their nestlings (Stallcup and Woolfenden 1978). Thus, they may be pre-adapted to differentiate between animal and plant foods.

Food choice depending on food availability

Consistent with prediction 2.a (Table 1), suburban parents showed a stronger preference for natural foods than did wildland parents. Suburban jays might show a higher

Table 3 Results of repeated measures ANCOVA for the proportion of waxworms taken per trial depending on waxworm handling time, habitat, supplementation, brood size, and group size

Source	Type III Mean square	*df*	*F*	*P*
Within-subject effects				
Handling time	7.789	1	8.215	0.007
Handling time–habitat	4.879	1	5.146	0.030
Handling time–supplementation	2.524	1	2.662	0.112
Handling time–brood size	0.087	1	0.092	0.764
Handling time–group size	2.420	1	2.553	0.120
Error (treatment)	0.948	33		
Between-subjects effects				
Habitat	5.319	1	3.638	0.065
Supplementation	7.827	1	5.353	0.027
Brood size	0.205	1	0.140	0.711
Group size	1.892	1	1.294	0.264
Error (treatment)	1.462	33		

We removed the non-significant handling time–habitat–supplementation interaction

preference for natural foods because the availability of these foods is lower in the suburban environment than in the wildlands. However, in contrast to this interpretation and to prediction 2.b, food supplementation increased jays' preference for natural foods. Our food supplementation might not have been sufficient to alter the jays' perception of the abundance of lepidopteran larva in the environment. In addition, supplemented jays might have been habituated to waxworms and consequently took more of this food type than non-supplemented jays.

Prediction 2.c was supported; regardless of food supplementation, preference for natural foods was greater when the jays fed the food to the nestlings rather than when self-feeding. The preference for natural foods to feed young, as compared with food choices for self-feeding, likely reflect the different nutritional needs of nestlings and adults. Nestlings grow rapidly (Starck and Ricklefs 1998) and have immature guts, hence extract less nutrients than adults (Karasov 1990), and are more likely to suffer from the consumption of low-quality foods than are their parents.

Food choice depending on time constraints

Consistent with prediction 3.a, preference for natural foods decreased with increased handling time in both habitats. In addition, suburban parents were more likely to choose waxworms, even if the handling time for this food type had been increased. Suburban parents might increase their efforts to provide nestlings with preferred food items because the availability of natural food is reduced in the suburban habitats and the experimental choice provides a ready source of those scarce foods. Furthermore, the nutritional demands of suburban adults are easily met by human-provided foods; thus, the additional effort may not be costly. Food supplemented blue tits (*Paruscaeruleus*) exhibited increased food selectivity and brought larger items to the young than did control birds (Grieco 2001). In support, Fleischer et al. (2003) reported that the foraging efficiency of suburban scrub jays in the 2 months before the onset of breeding was greater than that of wildland birds because of the access to the abundant human-provided foods. In contrast, wildland birds can readily obtain arthropods from the environment and may be less willing to invest additional effort in obtaining an otherwise abundant food when the handling time was increased. Prediction 3.b also was supported; regardless of the handling time required to obtain natural foods, they were more preferred for feeding nestlings than when the adults were self-feeding.

Our results do not completely explain why suburban Florida scrub-jays feed human-provided foods to nestlings. We found that parents in both habitats feed nestlings human-provided foods despite a strong preference for feeding nestlings natural foods and despite having ad libitum access to food for self-feeding. The experimental results are consistent with our observations in the field, where approximately 15% of the diet of suburban nestlings is human-provided foods (Sauter et al. in preparation). Our handling time treatment, which added only 1–2 s to the time necessary to obtain waxworms, may not have been

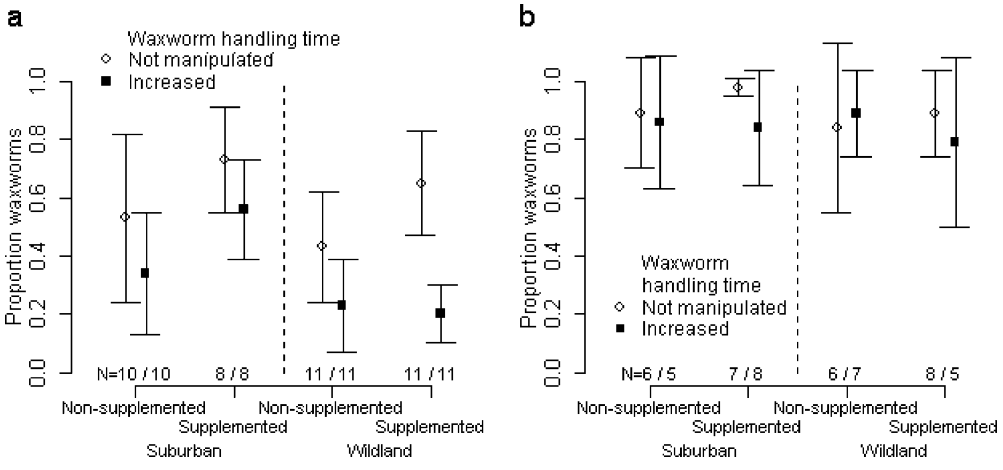

Fig. 2 Proportion of waxworms (natural food, ±SD) (**a**) taken at the feeder and (**b**) taken to the nest depending on habitat, supplementation and waxworm handling time. *N*=number of groups tested. *N* is smaller in items taken to the nest (**b**) than taken at the feeder (**a**) because birds did not take food to the nest in all groups

comparable to the increased searching time necessary for suburban jays to find arthropods in those habitats. Yet, despite the small increase in potential cost, adults switched their own diet from waxworms to peanuts, although they continued to feed nestlings mostly waxworms.

In general, the ecological conditions in the suburban habitat of reduced availability of preferred and high-quality arthropods and increased availability of less preferred and lower quality human-provided foods might result in parents providing nestlings with human-provided foods. This is especially true given the number of changes that occur with urbanization that might influence parental food selectivity. Optimal foraging models for central place foragers (Orians and Pearson 1979), such as parents provisioning young, predict that under the following ecological conditions it can be adaptive to reduce travelling times by foraging closer to the nest and thereby reducing food selectivity: 1) when faced with an increased starvation risk because of excessive brood demand, 2) when foraging time is limiting, and 3) with increased predation risk. Models by Houston and McNamara (1985a,b) show that to avoid starvation and when time for foraging is limited the frequency of feeding can be increased adaptively by decreasing food selectivity.

Suburban jays may have a relatively large mean brood size given the environmental quality of the suburbs. Suburban jays breed earlier and lay larger clutches than their wildland counterparts (Bowman and Woolfenden, unpublished data). Although brood sizes are the same in suburban and wildland habitat, the differences in the availability of preferred (natural) and less preferred (human-provided) foods, suggest that the optimal brood size in the suburbs should be smaller than the wildlands. Suburban pairs also have fewer helpers than wildland pairs (Bowman, unpublished data). The lack of helpers in suburban groups might contribute to some time limitation of suburban birds, because helpers feed nestlings and engage in territorial defense (Stallcup and Woolfenden 1978). Martindale (1982) predicted that if the costs of leaving the nest unattended are high, it should be adaptive for parents to decrease food selectivity and forage nearer to the nest. In urban areas, the density of both birds and potential nest predators may be higher than in wildland habitats (for details, see Kjoss and Litvaitis 2001; Haskell et al. 2001). In our suburban study area, nest predation risk increases with human density (Thorington and Bowman 2003) and predation rates on jay nests with nestlings are significantly greater than in the wildlands (Bowman and Woolfenden 2001). Hence, suburban parents might be more likely to forage on foods that are easily found and obtained, such as human-provided foods, even though they may be less limited in their provisioning ability than wildland parents and, therefore, feed human-provided foods to their young.

However, these mechanisms do not explain our observation that wildland jays normally do not feed human-provided foods to nestlings, but did so in our experiment. At the feeder, human-provided foods were probably more abundant and faster to handle than in the wildland environment. Houston (1985) suggested that an increased capture rate with the less preferred food type could lead to a partial preference for the less preferred food. Hence, the feeding of human-provided food to nestlings could be caused by an increased encounter rate with this food in both habitats. It is also possible that even in wildland habitats that are fire-suppressed, where nest predation is high (Woolfenden and Fitzpatrick 1984), birds tend to exploit predictable foods; however, we did not measure variation in this behavior relative to time since fire in the wildlands.

Even in our experimental trials where preferred foods were easily available in both habitats, 10% of the items fed to nestlings were human-provided foods. Observations in the suburbs suggest this proportion is actually somewhat larger (around 15%). This amount of lower-quality foods might be sufficient to significantly reduce diet quality. Other studies have shown that nestling growth can be highly susceptible to variation in protein (e.g., Japanese quail, *Coturnix coturnix japonica*, Marks 1993) and fat content (e.g., house martin, *Delichon urbica*, Johnston 1993). Although some of the human-provided foods have relatively high levels of both proteins and fats (Table 2), the digestive abilities of nestlings may not be sufficient to exploit them. In addition, birdseed contains 3–12% water (Diaz 1989), while an average insect contains 70–75% water (Bell 1990). Suburban nestlings might be more prone to dehydration and more susceptible to its effects because mean ambient temperatures are approximately 3°C higher in the suburban habitat than in the wildlands (LeClair 2005), and temperatures generally increase with urbanization (Kalnay and Cai 2003). In another experiment on jays at our natural site, Reynolds et al. (2003) found that food supplemented wildland females increased the amount of water but not fat allocated to eggs, indicating that water may be a critical resource for nestling development.

In summary, scrub-jays clearly discriminate between high- and low-quality foods, but their preferences change relative to breeding stage, likely depending on differing nutritional demands. When the availability of preferred, high-quality foods is experimentally decreased, adults switch to lower quality foods that are readily available; however, this is true only when self-feeding. When feeding nestlings, jays attempt to feed mostly arthropods. Despite this preference, in our experimental trials, both wildland and suburban birds still fed their nestlings 10% human-provided foods. Outside of our experiments, we observed that wildland birds never feed nestlings human-provided foods or even natural plant-based foods, but that in the suburbs the proportion of human-provided food is slightly higher than found in our experiments (15% vs 10%, Sauter and Bowman, unpublished). Large brood sizes relative to the reduced arthropod abundance in the suburbs may decrease the food selectivity of adult jays so that they can meet the demands of the brood. Consistent with the optimal foraging theory, they include lower quality foods in the nestlings' diet, even without changing their preference for high-quality arthropods. This study shows further that it is

difficult to predict the behavioral responses to urbanization, because urbanization changes a variety of habitat characteristics at the same time, and these characteristics might interact. This study suggests that the increased availability of human-provided foods and the decreased availability of natural foods influence food choices in the suburban habitat.

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